

VOICE AND LARYNX IN AFRICAN AND ASIATIC COLOBIDAE

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(With 2 text-figures)

SUMMARY

Laryngeal specialisation is a feature of the Primate family Colobidae. In an attempt to discover how far this may be correlated with vocal performance, extant field notes on voice have been summarised, and compared, so far as possible, with new material. The principal anatomical features of the larynges of seven genera are outlined.

Procolobus, in its alto utterances, associated with a small relatively unspecialised larynx, lacking sacculles and accessory sacs, stands isolated from the other genera. On the other hand the larynx of *Colobus (sensu stricto)* is especially large, lacks an air-sac, but shares with its Asiatic congeners the deep resonant voice and the presence of a subhyoid sac and laryngeal sacculles. *Presbytis*, while similar anatomically to its Asiatic congeners, emits a unique chuckling call; its larynx is very small. These preliminary results at once emphasise the close relationship of true *Colobus* to the Asiatic genera and the apartness of *Procolobus*.

INTRODUCTION

In a paper on the anatomy of the Olive Colobus Monkey (Hill, 1952) it was noted that details of the animal's utterances were not available, and that consequently laryngeal structure could not be interpreted in terms of function. The Olive Colobus is by no means unique in this respect, as we discovered during this investigation, the recording of details of mammalian voices is as yet in an unsatisfactory state. The family Colobidae are, however, of exceptional interest in their laryngeal anatomy, particularly with regard to the presence of accessory sacs in some members of the group. We have therefore collected all the available data on Colobid utterances, and examined preserved larynges of the following genera: *Colobus*, *Procolobus* (including *Piliocolobus*), *Semnopithecus*, *Kasi*, *Trachypithecus*, *Presbytis*, and *Nasalis*. The results for the Asiatic forms have been obtained from the collections and field notes of W. C. O. H., supplemented by data from the literature. The African forms have been investigated by A. H. B. in Ghana (the Gold Coast); anatomical notes were checked by W. C. O. H.

THE REPRESENTATION OF ANIMAL UTTERANCES

The problem of representing in print the vocal performances of animals is one to which little serious attention has been paid. Writers who mention animal utterances are apt each to choose his own method, and they generally record their observations in terms of the vowels and consonants of their own language. Confusion results from the lack of standardisation, as may be seen by reference to almost any book on the natural history of birds.

Adoption of the standard international phonetic symbols would seem to be an elementary step towards clarity and consistency. Even these, designed as they were to represent human phonation, are often far from adequate to denote the performance of a differently constructed larynx, still less that of a syrinx. Nevertheless, together with notes on pitch and quality, they can provide a much closer approximation than do the casual transcriptions so commonly published.

In recent years, conscientious ornithologists have attacked the common use of consonants in the transcription of bird calls, particularly the labial *p* which, for a bird, is an anatomical impossibility. The same sort of criticism is generally valid for representations of mammalian utterances, not so much in this case on anatomical grounds, but rather due to inaccurate observation or to misleading linguistic convention.

Such a conventional use of consonants has its roots in onomatopoeic names, which are common in every language. The same conventions sometimes apply in languages of very different structure. For example, *k* is used at the beginning of a syllable to indicate that the vowel immediately following begins at full volume, *m* that it begins softly, *ch* (*t*) that it is harsh, and so on. *k* is also used to indicate a break between two syllables, as in the English 'cuckoo'. Phonetically, the cry of the bird approximates to 'u ? u:', and it is best imitated by the human voice if the glottal stop is used as indicated between the two syllables. Certainly the consonantal *k* is incorrect. An exactly analogous case is the Ashanti onomatopoeic name for the monkey *Cercopithecus lowei*: the root of the name is 'kwaku', the cry 'a ? u:'.

Consonants used in this way will here be called *indicator consonants*. The main disadvantage of their use in describing the utterances of a monkey lies in the fact that the animal may indeed be capable of producing genuine consonants. If an observer in recording a call uses indicator consonants, it is impossible to tell, without further information, whether consonants are uttered or not.

In this paper, we have necessarily admitted indicator consonants where the data are drawn from the literature, or where our field notes had been taken before the phonetic transcription had been contemplated. But wherever possible, the cries of the monkeys are recorded first phonetically, with notes on pitch, volume, and quality, and then in English transcription, using indicator consonants.

THE VOICES OF COLOBIDAE

Our knowledge of Colobid utterances suffers from the fact that these monkeys, and more particularly the African forms, are exceedingly diffi-

cult to keep in captivity; and, whilst it is an admittedly important principle that all calls heard in captivity should be checked against field records, the captive specimen is a most useful subject. Not only does it enable the transcription of the call to be checked, but it also gives what is apt to be all too rare in the field, a view of the animal during phonation, unimpeded by the forest foliage or by the necessity for concealment.

Colobus polykomos. This species has been studied as representing the Black Colobus *Formenkreis*. No differences have been observed between the calls of the three subspecies *polykomos*, *dollmani*, and *vellerosus*. The voice is at once distinguished from those of the Red and of the Olive Colobus (genus *Procolobus*) by its deep pitch and great resonance.

The full call of the Black Colobus is characteristically uttered by the male. It may easily be represented phonetically as 'ə: ə: ə: ə:'. About five to ten syllables are normally uttered, the full duration of the call being about seven to fifteen seconds. There is a distinct rise in pitch and volume both within each syllable and throughout the call as a whole. Beginning about $2\frac{1}{2}$ octaves below Middle C, each syllable represents a rise of something over a semitone in pitch. In quality, the call resembles a human bass voice straining below the lowest pitch in its register, but it has the great resonance noted above, which prevents its being called a 'grunt'. Even within the closed forest, the call can be heard from a great distance. A suitable English rendering would be 'urr rurr rurr rurr'. The full call would seem to have the same sort of significance as in monkeys and apes in general. Usually, if not invariably, uttered by an adult male, it may be heard in the absence of any apparent external stimulus. In such cases it may be interpreted as an assertion of status by the overlord of a troop. It is, however, also used in defiance, particularly in the presence of the Crowned Hawk-Eagle, *Stephanoaëtus coronatus*. Similar behaviour on the part of a mangabey *Cercocebus albigena* has been recorded by Malbrant and Maclatchy (1949).

The alarm-call, which may precede the full call uttered in defiance but is more often heard alone, is common to all ages above the infant, and to both sexes. It takes the form of an explosive snort, uttered partly through the nose. Phonetically it approximates to 'tnr'.

These two cries might be considered to be the only fully social utterances of the Black Colobus. The remainder are of a more intimate nature, having significance apparently either to the utterer alone, or to its immediate neighbour (mother, offspring, rival, etc.).

When mortally wounded, the Black Colobus utters isolated, resonant croaks, similar to the syllables of the full call. This observation applies to adults of both sexes.

Occasionally, when the observer is within a very few yards of an unsuspecting troop, a very soft grunting may be heard. This call has about the same initial pitch as the full call, but lacks both the resonance and the rise in pitch when repeated. It is easily confused with a similar sound of different significance uttered by the male of *Cercopithecus petaurista*. Only one specimen has been shot while making the call. This was a lactating female. Though apparently intimate, the call has not been heard in captivity.

The only other adult call recorded consists of a series of snorts uttered at about $\frac{1}{2}$ -second intervals. These are quite irreproducible in print, but recall the noise made by a pig excitedly rooting. In the field, the call

has only been heard when two individuals quarrel, or when a wounded specimen on the ground is approached. In captivity, it is the call most frequently uttered, both by adult and subadult specimens down to about one year old. It seems to indicate any kind of excitement, not necessarily anger or defiance. It can be imitated to good effect by hunters, who thereby induce the monkeys to show themselves, apparently in curiosity.

The calls of the young Black Colobus are not detailed here. They include a variety of screams and other intimate and often pathetic noises. The ability to grunt at a very low pitch is acquired within a few months of birth.

Procolobus (Piliocolobus) badius. The two races *P. b. badius* and *P. b. waldroni* have been studied; they have closely similar vocal capabilities, and the species is notable for its apparent inability to remain silent for any length of time. Often uttered from the tops of the highest trees, its monosyllabic call is very bird-like when heard from a distance. At closer range, however, it has a much more human quality.

The basic call, from which all the others are apparently derived is 'jau[?]', pitched in the octave below Middle C. An English version with indicator consonants would be 'kyowp'. (Natives of Guiglo, Ivory Coast, nickname the species 'kyow-kyow'). All the variants of this basic call can be imitated with great accuracy and without strain by the human female.

The basic call is uttered most frequently, most loudly, and at its highest pitch in the presence of an intruder, whether human or animal. Even under comparatively peaceful circumstances, however, the effort put into the act of phonation is considerable. The vocal individual can, indeed, be identified at a distance by the shaking of the surrounding vegetation.

When a fight is in progress, the combatants' utterances may become more abrupt and ferocious or (perhaps in the case of the loser) more drawn-out and feline. In the latter case, the glottal stop is absent thus: 'iau:'. The English version of this call is 'yow'.

An utterance less frequently heard is a simple 'au' (English 'ow'). The quality and pitch of this sound are those of the human female at a rather low point in her register. It is neither very emphatic nor very loud, and is often interspersed in a series of loud 'kyowp' calls, as if the utterer were exhausted by the effort. The only two specimens obtained while uttering this call were adult males.

The last variant of the basic call is very rarely heard. Our two field records appear to suggest that it is part of a deliberate act of defiance by the overlord male of a troop. In both cases the troop had been pursued without shooting, in an attempt to isolate the nursing mothers. After a considerable distance had been covered, the dominant male abandoned the upper canopy and descended to within one hundred feet of the ground, pacing up and down in an agitated manner and constantly looking down at the hunters. The cry uttered was a fierce and at the same time drawn-out variant of the basic call, something between a howl and a bark in quality.

The Red Colobus is both unusual and limited in its vocal range. Although the adult calls do apparently include expressions of alarm, defiance and more casual intercommunication, they are all variants of a single

simple utterance. The cries of infant and juvenile stages have not been studied in detail, as such specimens rarely survive more than a few days in captivity, while the volume of the cries is so feeble that in the field they can only with difficulty be heard at all. It is interesting to note, however, that a distinct consonant has been heard in one of the calls of the infant Red Colobus. The call is a bird-like 'tju' or 'tjau'. In view of this observation at close range, it must be regarded as possible that the consonant is also used by adult monkeys on some occasions, but remains undistinguished at treetop height.

Procolobus verus is but poorly known ecologically and ethologically. The opportunity is here taken of modifying certain impressions of its habits which were reported in the earlier paper (Hill, 1952). In Ghana and Ivory Coast, the species appears to be neither rare, omnivorous, nor solitary. It is, however, both shy and silent, alike in its progress through the thick undergrowth and in its reluctance to use its voice. It lives in parties of from 5 to 20 individuals, which are most frequently to be found feeding in company with the much noisier Cercopithecids, *C. mona*, *C. campbelli*, or *C. petaurista*. Communal feeding does not imply a common diet, since the Olive Colobus remains true to type in eating only leaves. The above remarks will be expanded elsewhere, but for the present purpose they serve to explain the paucity of observations and the remarkably limited use of the voice.

Apart from screams of terror, the only call of this species which can be regarded as satisfactorily recorded is a truly remarkable utterance. The call is 'u: u: u: u: iaʊ iaʊ ui: ui: iaʊ'. It rises steeply in pitch and volume to the penultimate syllable, and dies away on the last. In English it may be rendered 'hoo hoo hoo hoo yow yow wee wee yow'. The call may be complete, or only a part of it may be uttered. In neither case is its significance clear. Like the calls of the Red Colobus, it is alto in pitch and almost human in quality until the climax, when it degenerates into a scream. The whole effect is more like the cry of a Chimpanzee than that of a monkey, especially when several members of the troop are calling at the same time. The relationship to the call of the Red Colobus is, however, clearly audible in the 'yow' syllable, which is, very rarely, uttered alone.

No definite alarm call has been heard from this species, even when a troop has been surprised in the absence of Cercopithecids. There is little doubt that the silence of the Olive Colobus is correlated with its frequent association with these Guenons. The latter, being largely fruit-eaters, are of a much more active and inquisitive disposition when feeding, and are almost invariably the first to spot an intruder. Their alarm calls are, moreover, apparently understood and acted upon by the Olive Colobus. This behaviour is in contrast to that of the Red Colobus, which, feeding generally at a much greater height, is normally seen to disregard the activities and utterances of the Cercopithecids, and sometimes even those of the Black Colobus.

The most striking feature of the calls of the African Colobidae as a group is their lack of close and obvious interrelationships. The Black Colobus especially is widely separated from its relatives.

As between Cercopithecids, by contrast, there is a very distinct common pattern to the vocal performances of the various species. This has been remarked upon by Hadow (1952). In West Africa, for example the calls

of *C. mona* and *C. campbelli* are, though interdistinguishable, closely related. *C. petaurista* is a little more distant, and *C. diana* still more so. *C. aethiops* is altogether harsher, and lacks any musical notes. *Erythrocebus patas* is still recognisably *Cercopithecus*-like. But between the Guenons and the Mangabeys (*Cercocebus* spp.) there is virtually no comparison.

Of the Colobus monkeys, it is clear that the Olive and the Red species are least different in their vocal range. The degree of difference is hard, to judge, but if a comparison with the Guenons may be taken as a guide the difference between the calls of the Olive and the Red Colobus is at least equal to that between the calls of *Erythrocebus* and of any *Cercopithecus* sp. From both the Red and the Olive Colobus the Black Colobus is separated by a gap at least as wide as that between *Cercopithecus* spp. and *Cercocebus* spp.

Semnopithecus entellus. Considering Blanford's remark (1888) that 'Few, if any, wild animals afford better opportunities for observation than the Hanuman Monkey', there is very little information about its voice. The same author goes on to describe two calls. The first is 'a joyous, musical "whoop" uttered in motion, used chiefly at dawn and dusk,' and the second 'a harsh, guttural alarm-note'. Stripping the former call of its indicator consonants, it may well correspond to the full call of the Black Colobus, though the African species has never been observed to utter the full call in motion.

Semnopithecus schistaceus. 'The call is "hoop, hoop", generally uttered as a warning cry by one of the troop', Pocock (1939). This cry is doubtless almost identical with that of the Hanuman recorded above.

Semnopithecus priam. The voice of the male of this species is a deep 'u:', several times repeated. In English this may be written 'boom'. Each syllable is of longer duration than in the rather similar call of *Kasi senex*. In quality, the note is like the bay of a foxhound, but the pitch is rather higher. There is also a conversational whine, used more by females and juveniles.

Kasi johnii. Blanford describes this species as very noisy, having a long loud full call and a low, guttural alarm call, used also in anger. Kinloch (1923) gives the full call, as 'hoo-ha hoo-ha hoo', uttered at any time of the day. As already noted (Hill, 1937), the roaring full call is like that of *K. senex monticola*. The double 'hoo-ha' recorded by Kinloch appears to be one of the effects of great resonance of the voice; phonetically it approximates to 'uəa:'. There is also a short, sharp growl, probably the alarm call noted by Blanford, and a whining note used by females and juveniles.

Kasi senex. Phillips (1935) gives the call of the male as 'hoo hoo hoo hoo.' He also reports a shrill squeak indicating curiosity, and a bird-like twitter expressing pleasure or excitement. W.C.O.H. has confirmed these observations. The male full call is deeper, more throaty and more sharply cut off than in *Semnopithecus* spp. It is seldom heard in captivity, though the squeak and twitter are frequently used.

Trachypithecus pileatus. McCann (1933) mentions a harsh bark, interpreted as an alarm call, and a squeaking noise.

Trachypithecus phayrei crepusculus. Tickell (MS), quoted by Blandford, states that the short, deep bark of this monkey resembles that of *Semnopithecus entellus*.

Trachypithecus obscurus. The voice is similar to that of *Kasi senex*. There are two versions of the alarm-call. The shorter is a sharp 'tnʌ?', English 'chāk'. At other times a disyllabic call is used thus: 'tnʌ?ɔ:' English 'cha-hau'.

Trachypithecus cristatus. Banks (1931) notes that a young captive specimen of the typical race uttered plaintive, gibbon-like squeaks. The alarm-call of *T. c. pyrrhus* is given by van Balen (n. d.) as 'ki cha hau' (Dutch). Forbes (1897) quotes onomatopoeic native names collected by Hose as follows: Dyak - 'bigok'; Kayan - 'chikok'. These are clearly versions of the alarm call which seems to be characteristic of the genus.

Presbytis femoralis. van Balen gives the native name as 'gyak-gyak', which is presumably an imitation of the alarm call. Banks likens the noisy staccato chuckle of *P. f. chrysomelas* to that of a giant squirrel (presumably *Ratula bicolor*).

Presbytis melalophos. van Balen transcribes the cry as 'kjèk kjèk kjèk kjèèèk kjèèèk kjèk kjik kijk' (Dutch).

Presbytis frontatus, P. hosei, P. everetti. Banks finds the 'loud chuckles' similar to that of *P. femoralis*, but notes also that *P. hosei* and *P. everetti* utter a snorting sound similar to that of *Nasalis*.

Presbytis rubicundus. This species has a scolding, truculent cry, and, according to Banks, another call which is a series of loud, resonant chuckles; the first note of the latter is as in *P. f. chrysomelas*, the succeeding four sharper and shriller.

Nasalis larvatus. Hornaday (quoted by Forbes, 1897) gives the cry of the Proboscis monkey, presumably the full male call, as 'honk' or 'kec-honk'. Shelford (1916) refers to it as a 'sort of snorting bark' and believes that the fleshy nose plays a part in its production. Banks states that anger is expressed by a loud, resonant snore uttered with opened mouth. He also remarks that inhalation and exhalation through the nose are audible at some distance. The female has a petulant cry, faintly resembling that of a goose.

COMMENTS ON VOICE

Despite the heterogeneity of the above observations, certain patterns of vocal capabilities emerge. Firstly there is the undoubtedly aberrant performance of *Procolobus verus*. The restriction of the utterances of this species to alto and treble pitch even in adult males is especially noteworthy. There is no evidence of the typical bark or even a snort.

What we have referred to as the full call, emitted typically by the dominant male, would seem to have a common pattern in *Colobus*, *Semnopithecus*, *Kasi*, and *Trachypithecus*. This consists of a series of simple repeated syllables of great resonance. The generally monosyllabic

alarm call is also rather closely similar in all these genera, and probably *Nasalis* falls in here, though data are at present insufficient relative to this genus.

Presbytis appears to be unique in its ability to produce a chuckling sound. Such calls are common in mangabeys and macaques, but have not been recorded in any other Colobid genus.

The squeaks and screams recorded at various points in the account are, of course, common to all young monkeys. But the twittering sound reported in *Kasi* appears to be peculiar to that genus.

LARYNGEAL ANATOMY

This account of the comparative anatomy of the Colobid larynx is largely supplementary to that already given elsewhere (Hill, 1952).

Dimensions. The measurements given in Table I reveal that *Colobus polykomos* possesses by far the largest larynx of those measured (the size is equal to that of an adult human male). At the other end of the scale, *Procolobus verus* and *Presbytis femoralis* both have very small larynges. *Procolobus badius* has a slightly larger one, but the organ is still distinctly inferior in size to those of the remaining Asiatic genera, which are remarkably uniform in this respect.

TABLE I

Dimensions of Colobid larynges. Adult Males.

	Length	Diameter	
		Dorsoventral	Transverse
	mm.	mm.	mm.
<i>Colobus polykomos vellerosus</i> ...	59	36	34
<i>Semnopithecus priam</i> ...	36	23	21
<i>Kasi s. senex</i> ...	39	20	20
<i>Trachypithecus obscurus</i> ...	35	21	21
<i>Presbytis thomasi</i> ...	16	13	12
<i>Nasalis larvatus</i> ...	36	20	24
<i>Procolobus verus</i> ...	20	12	14
<i>Procolobus badius waldroni</i> ...	24	16	15

The hyoid apparatus. Throughout the Colobidae, the corpus hyoidei has the shield-like shape common to all Catarrhine monkeys. This shape is generally associated with the presence of some kind of subhyoid sac opening into the larynx at the base of the epiglottis. The convexity of the shield is disposed antero-ventrally, its concavity towards the vestibulum laryngis (Fig. 1B). Despite the absence of a subhyoid sac in the genus *Procolobus*, the shield-shaped corpus hyoidei persists; the bone is, however, of relatively solid structure.

The anterior cartilages. The epiglottis is broad in all Asiatic genera and in *Colobus*. As already noted (Hill, 1952), it is relatively broader in *Procolobus verus* than in *P. badius*, but in both species it narrows appreciably towards the tip. In all genera, it is placed at a pronounced angle to the axis of the thyroid cartilage; this angle is often almost a right angle, but its variability is doubtless in part due to the process of

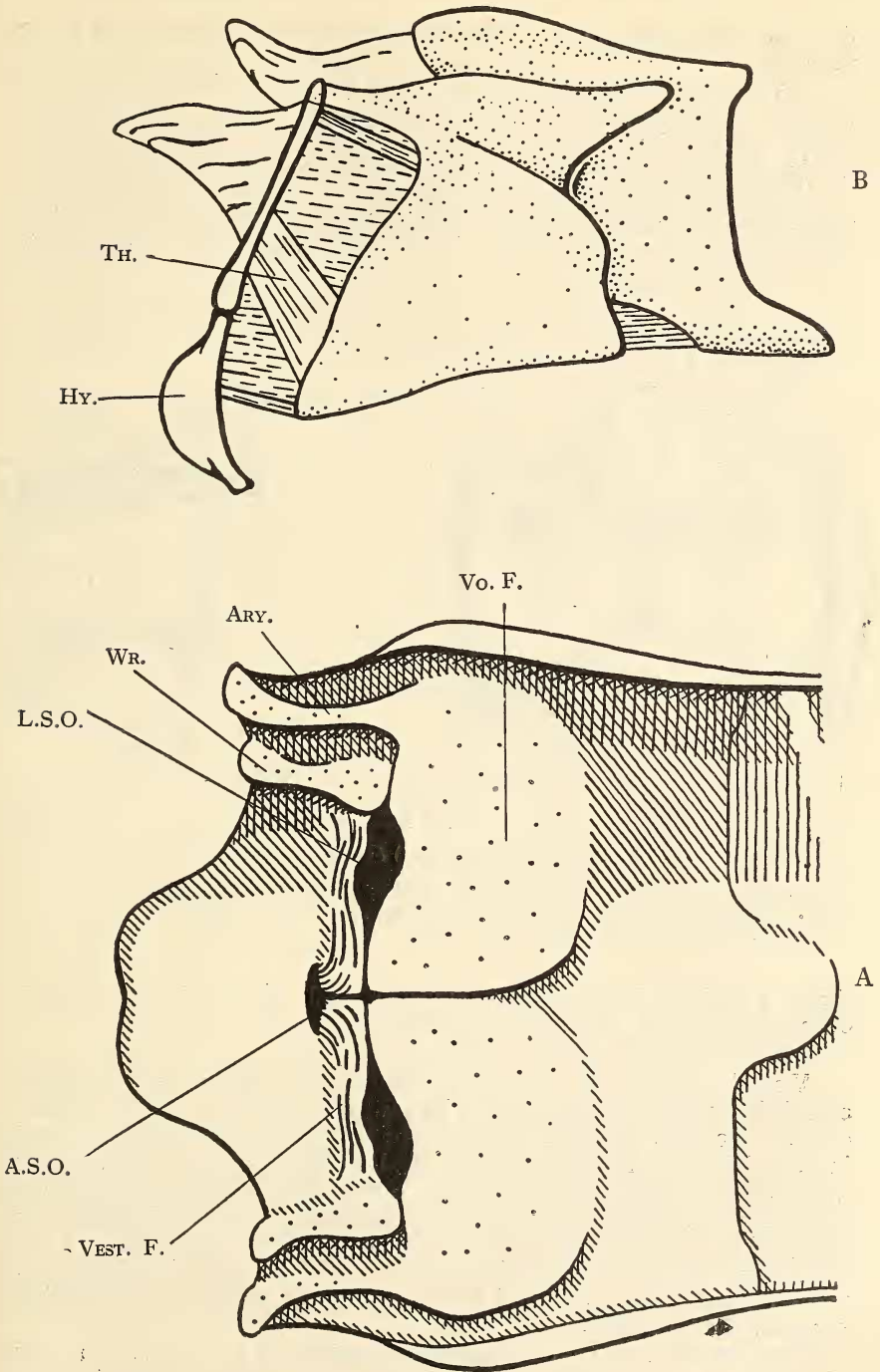


FIG. 1.

Colobus polykomos vellerosus

Larynx of the adult male,
 A: opened by a median dorsal incision to show internal features; B: in left lateral view
 Ary=Arytenoid cartilage; A. S. O.=Air-sac opening; Hy=Corpus hyoidei; L.S.O.=
 Opening of laryngeal saccule; Th.=Oblique thickening of thyro-hyoid membrane; Vest.
 F.=Vestibular fold; Vo. F.=Vocal fold; Wr.=Wrisberg's cartilage.

fixation. The epiglottis thus forms an almost complete, mobile roof to the vestibule.

The free margin of the epiglottis is entire in *Semnopithecus*, *Kasi*, and *Presbytis melalophos*, slightly notched in some specimens of *Trachypithecus obscurus* and of *Procolobus*, and distinctly notched in *Nasalis*. In *Colobus* and in *Presbytis thomasi* there is a broad, shallow depression at the tip.

Wrisberg's cartilages are markedly swollen in all the forms investigated, with the sole exception of *Procolobus badius*. In this species, they hardly project from the aryepiglottic fold (Fig. 2). Of the remaining forms

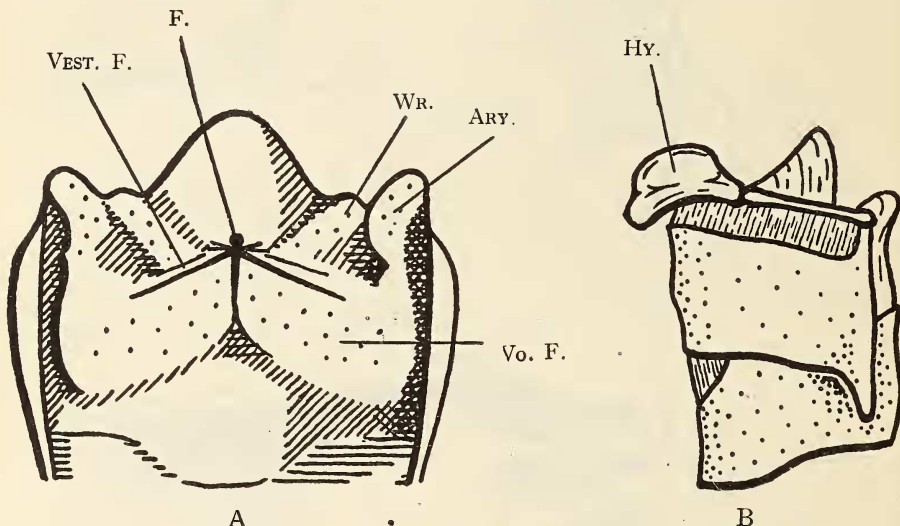


FIG. 2.

Procolobus (Ptilocolobus) badius waldroni.

Larynx of the adult male drawn as the corresponding views in fig. 1.

F. = blind fossa in position of air-sac opening.

Other references as in fig. 1.

they are perhaps least developed in *Kasi* and *Trachypithecus*, though even here they are unusually prominent.

Vestibular folds. These organs are usually well defined, especially towards the mid-ventral line, where they are sharply demarcated. They are, however, inclined to be feeble in *Presbytis thomasi* and in *P. melalophos*. In *Colobus* the vestibular folds are blunt-edged, having a loose, fleshy appearance (Fig. 1A). The ventral (median) extremities of the vestibular folds of the two sides are separated in all Asiatic genera by the opening of the subhyoid sac. In *Colobus*, the extremities of the vestibular folds are continued into the walls of the sac. In *Procolobus*, where the sac is absent, a blind fossa in the same morphological position separates the folds (Fig. 2A).

The main part of the opening of the subhyoid sac is more or less slit-shaped in *Presbytis*. In *Semnopithecus*, *Kasi*, *Trachypithecus*, *Nasalis*, and *Colobus* (Fig. 1A), there is at the anterior end of the median slit a transverse extension, giving the opening a T shape. The transverse

limb of the T effectively defines the cranial border of the vestibular folds, hence the feeble definition of these folds in *Presbytis*.

Subhyoid sac and air sac. In all Asiatic genera studied, both these structures are present. The subhyoid sac opens into the larynx by the generally T-shaped opening described above. It then expands to a capacity of some few millilitres beneath the concavity of the corpus hyoidei. Its expansion is limited particularly by the oblique ligamentous thickenings of the thyrohyoid membrane (Fig. 1B), and by the corpus hyoidei itself. *Colobus* resembles the Asiatic genera in this respect.

In the Asiatic genera the subhyoid sac ventrally takes a turn caudad as funnel-like passage, piercing the thyrohyoid membrane and deviating to the right to bypass the stratum of the infrahyoid muscles. Thereafter, it expands in the subcutaneous areolar tissue to form the main portion of the air sac, which extends over the base of the neck to the clavicular region, and anteriorly as a saccule in the interramal region. In a female of *Kasi senex nestor*, a cast of the uninflated air-sac displaced 35 ml. In life, the sac is capable of much greater inflation, standing out as a goitrous body in the neck. Inflation and deflation are possible without accompanying phonation. The platysma myoides overlies the sac superficially and doubtless serves to deflate the organ.

In *Colobus*, the subhyoid sac is not continued into an air sac, the thyrohyoid membrane being nowhere pierced. In *Procolobus*, there is no subhyoid sac. The blind fossa noted above doubtless represents a vestigial subhyoid sac, which has become reduced simultaneously with the larynx as a whole.

Laryngeal saccules. These structures are blind, inextensible upgrowths of the ventricle, which resemble those of the human larynx. They do not become extra-laryngeal as in Apes, but they are relatively larger than those in Man, except in *Procolobus*, where they are very much reduced. The openings of the laryngeal saccules, bounded by the vocal and vestibular folds, are narrow and slit-like in the Asiatic genera, and extremely so in *Procolobus*. In *Colobus*, they are quite broad and irregular in shape (Fig. 1A).

Vocal folds. *Colobus* is unique in possessing vocal folds with a blunt, curved anterior edge. In the Asiatic genera, the vocal folds are straight and sharp-edged, as in *Procolobus*.

In laryngeal anatomy, as in voice, the genus *Procolobus* in many respects stands isolated from *Colobus* and from the Leaf-monkeys of Asia. The reduction of the subhyoid sac and of the laryngeal saccules are the chief points of difference. *Colobus* is intermediate between the Leaf-monkeys and *Procolobus* in one particular, namely the presence of the subhyoid sac without its extension into an air-sac. In the structure of its vocal and vestibular folds, however, it conforms to neither group, and must be considered aberrant.

DISCUSSION

It is evident that at this stage laryngeal structure and voice can only in the most general terms be correlated.

1. Size of larynx. The expected relationship between physical dimensions and depth of voice appears to hold good. In this respect there are three distinct groups.

a. Colobus. Larynx very large. Voice extremely deep.

b. Semnopithecus, Kasi, Trachypithecus, Nasalis. Larynx large. Voice deep, but not, apparently, as deep as *Colobus*.

c. Presbytis, Procolobus. Larynx small. Voice staccato, rather high pitched (*Presbytis*) or distinctly alto (*Procolobus*).

2. Subhyoid sac. The voices of all those genera possessing the subhyoid sac are described as 'resonant' by most observers. This observation is of particular interest in the case of *Presbytis*, in view of the small size of its larynx.

3. Air-sac. Negus (1949, p. 56) concludes that 'there is little evidence to support, but much to disprove, the generally accepted view that air-sacs are developed for the purpose of voice'. He suggests that the significance of practically all air-sacs (including the subhyoid sacs mentioned above) is that they enable air to be conserved during periods of intense activity, when it is not possible to bring into action the normal muscles of inspiration and expiration. Any vocal function they may perform is held to be purely secondary. This view is worthy of some discussion, since Negus's work is the most comprehensive on the subject of comparative laryngeal anatomy.

Since there is no muscular mechanism by which the air sac can be filled directly from the ambient atmosphere, the air with which it is inflated must come from the lungs. This is doubtless achieved by the following stages: (1) air is drawn into the lungs; (2) the oral and nasal passages are closed; (3) the lungs are emptied by a normal expiratory movement, and the air thereby forced into the air sac. The process may be repeated until the sac is fully distended. Finally, the lungs may be inflated in addition. The animal would then be ready, according to Negus's theory, to undertake a bout of strenuous activity.

There are, however, several objections to the above suggestion as to the function of the air-sac. In the first place, the sac will inevitably contain only expired air, with a relatively low oxygen and high carbon dioxide content. Secondly, if the normal respiratory movements are to be avoided during the period of intense activity, the only possible means of passing air between air-sac and lungs is the very slow process of mixing by diffusion, rendered even slower by anatomical considerations. It would be possible for the monkey without impairing its activity to perform a normal expiratory movement, and then perhaps to reinflate the lungs by deflating the air-sac. But since the mechanism for deflation is merely the weak platysma myoides, it is doubtful if there is any real support for this suggestion. Lastly, there is no indication that *Colobus* and *Procolobus*, which lack air sacs, are any less capable of violent or sustained activity than are the Leaf-monkeys. We therefore consider that the explanation of Negus as to the primary function of the air-sacs is unsatisfactory.

On the other hand, it is almost certain that any vocal significance which the air-sac may have is secondary. The position of the opening is such that only if air is breathed *in* from the sac will it pass over the vocal folds on its way out to the atmosphere. Air passing out directly through

the nose or mouth cannot itself be responsible for phonation, though it may modify the sound produced by air passing out from the lungs over the vocal folds in the normal way. In addition, the inflated air-sac almost certainly affects the resonance of Leaf-monkey utterances.

It has been remarked above that the air-sac is capable of inflation and deflation without any accompanying phonation. The performance has a marked effect on the appearance of the animal. It is thought likely that the action may have some social significance, and that this significance may be the primitive one.

On the other hand, the subhyoid sac, as noted above, would appear to be purely vocal in function. The resonance of the calls of the Asiatic genera might perhaps have been ascribed to the presence of the air-sac alone. But the air-sac is absent in *Colobus*, while the resonance of the call remains very great. The case cannot be regarded as proved, since the larynx of *Colobus* is exceptionally large, and would have resonance in its own right. No other possible function, however, suggests itself at present.

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